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Eye Movement during Sleep and Waking in Infant Monkeys (*Macaca mulatta*) Deprived of Patterned Vision[1]

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Eye Movement in Visually-Deprived Monkeys

Abstract

5 newborn rhesus monkeys deprived of patterned vision and 4 normal-sighted controls were reared until 18 months of age. There was a significant decrease in frequency of rapid eye movement (REM) with age in both groups. Frequency of REM tended to be lower in experimental monkeys than in controls. Asymmetries in velocity of waking horizontal eye movement were evident in experimental monkeys, and the velocity of REMs was less in pattern-deprived monkeys than in controls. Nonsequential interval histograms between REMs at 18 months of age differed significantly from a random exponential distribution in both groups. Pattern-deprived monkeys had significantly fewer short intervals between REMs than controls.

Infantile visual deprivation; eye movement; REMs; EOG; nystagmus; vision; sleep; rhesus monkeys.

The effects of restriction of visual input in the newborn on the developmental characteristics of rapid eye movement (REM) sleep have been the focus of a number of recent studies on blind humans (Amadeo & Gomez, 1965; Berger, Olley, & Oswald, 1962; Gross, Byrne, & Fisher, 1963; Offenkrantz & Wolpert, 1962) and kittens reared in darkness (Fishbein, Schaumberg & Weitzmann, 1966). In the earlier observations on blind humans (Berger, Olley, & Oswald, 1962), it was found that three men with life-long blindness and two men blind for 30 and 40 years, respectively, did not exhibit REMs during otherwise normal emergent EEG stage 1 sleep periods. REMs were observed to be present during the sleep of three men who had been blind for only 3, 10, and 15 years, respectively.

The purpose of the present study was to follow up these observations by depriving newborn monkeys of patterned vision, and to study the development of their eye movement characteristics during sleep and wakefulness, in comparison with those of a normally-sighted control group of similar infant monkeys.

Method

Subjects

The pattern-deprived group was composed of three male (#s 533, 576, & 713) and two female (#s 586 & 698) newborn, full-term rhesus monkeys (Macaca mulatta). Their gestational ages ranged from 158 to 168 days; their birth weights from 402 to 588 g. The control group consisted of two male (#s 605 & 641) and one female (#635) normally-sighted, full-term infants,

with gestational ages ranging from 157 to 165 days, and birth weights from 538 to 666 g. A fourth normally-sighted, full-term, male infant (#675) of 166 days gestational age and birth weight 680 g, served as an additional control for certain measurements taken when it had reached 18 months of age. All of the infants were delivered vaginally.

Procedures

The infants were separated from their mothers within ten hours of birth, following which the umbilical cord was tied and the infant bathed. With the exception of infant #533, translucent contact occluders were then inserted over the corneas of all experimental infants.

The occluders were made by using the bases of cellulose nitrate test tubes (IEC 655), 1.3 cm in diameter. The bottoms of the test tubes were dipped in a suspension of white opaque pigment (Turtox 380A797) in acetone, inverted and allowed to dry. An even white translucent surface was thereby deposited on the outside of each tube. The base of the tube was then cut off to form the occluder, and the edge and inner surface sanded smooth. Finally, the inner surface of the occluder was polished to a high finish with surgical gauze soaked with a buffing compound (Turtox).

The occluders approximated the corneal curvature of the newborn infant's eye very well and rarely did they cause any irritation, except for the case of infant #698. When this infant was one month of age, the left eye occluder fell out and a prominence of the anterior portion of the cornea, together

with some corneal clouding and capillary formation on the limbus were observed. This condition failed to respond to treatment with corticoids and antibiotics and developed into an entopthalmic condition, together with permanent scarring of the cornea. Since vision was irretrievably lost in this eye, occlusion no longer remained necessary.

The intactness of the occluders was checked at least twice daily at about 7:30 a.m. and 4:00 p.m. Infrequently, when an occluder was found displaced from the eye it was replaced immediately. Such displacements were estimated to have accumulated to no more than 12 to 24 hours of visual experience during the 15-month period of study in any one infant.

Monkey #533 experienced varied procedures of visual deprivation during its first five weeks of life. The eyelids of this infant were initially sutured together soon after birth. However, after four days the sutures no longer held the eyelids together in complete approximation and an opaque bandage was placed over the eyes. A second attempt was made 11 days later to suture the eyelids together, which again proved unsuccessful after four days. The infant was thereafter maintained in darkness until it was 35 days of age, at which time translucent contact occluders were inserted.

All infants were reared in continuous light on mother surrogates (Harlow & Zimmerman, 1959) placed in standard monkey cages. The infants were free to drink milk formula on demand until weaned, from bottles mounted at the top of

the surrogates. When the infants no longer clung to the surrogates, the surrogates were removed. This usually occurred around one year of age.

The recording procedures were similar to those used in an earlier study (Meier & Berger, 1965). All physiological variables were recorded from hypodermic needle electrodes inserted subdermally and affixed with collodion. Three 1/4 in -27 gauge needle electrodes were inserted into the scalp so as to form a right antero-posterior chain for the recording of the EEG; two were inserted at the outer canchi of the eyes, and one at the nasal bridge for recording the horizontal electrooculogram (EOG) of each eye. Two similar needle electrodes were inserted into the nuchal muscles for the recording of the electromyogram (EMG); and a fifth into the left ear for a ground. The EEG, EOG, and EMG were recorded on a Grass Model 5 polygraph or Model 6 electroencephalograph with paper speeds of 10 and 15 mm/sec, respectively. A relatively slow time constant of 1 sec was used to record the EOG in order to detect both slow and rapid eye movements. During the latter part of the study magnetic tape recordings were also taken using a Sanborn (2000 Series) or Ampex (FR1300) tape recorder.

Recordings were taken from the animals in a lighted, electrically and sound-shielded chamber while they clung to the mother surrogates. When they no longer exhibited this behavior, they were restrained in a cage by a plastic collar placed around the neck which allowed them to move only in a lateral direction.

Recordings commenced at about 10:00 a.m. and were terminated at about 5:00 p.m. The monkeys habitually slept in their home cages during the day and never established a prominent diurnal rhythm. This was undoubtedly due to their having been maintained in continuous light.

Owing to the length of the study, amounting to 2 1/2 years in collection of the data alone, it was not possible to adhere to a regular recording schedule common to all animals. Problems involving equipment scheduling and breakdowns, occasional ill health and transfer of the study from San Juan to Los Angeles often led to cancellation of scheduled recordings. As a general rule recordings were taken at one-to-two-week intervals until the infants were about six months of age, and thereafter monthly until 18 months of age.

The eye occluders were removed from the pattern-deprived animals at 18 months of age. The monkeys were then placed in darkness overnight to allow any corneal edema to dissipate. The following day behavioral tests of their visual abilities were performed. Similar visual tests were carried out in the control group at the same age. Polygraphic recordings were continued in monkeys #s 576 and 713 while maintained in continuous light for a further six weeks. A second series of behavioral tests were performed on these animals at 84 weeks of age.

Visual Testing Procedures

In addition to gross observations of behavior, particularly locomotion in a strange environment, the following tests were performed with the animals restrained in a small primate chair.

Pupillary Response. Pupillary contraction to a light shone directly into the eyes was tested.

Following Response. The presence of following movements of the head and/or eyes to a moving point source of light, a 12-in. diameter board composed of 1/2 in-wide black and white stripes, and a small brightly-colored object were investigated.

Blink Response. The investigator's hand was rapidly flourished from a distance of two feet up close to a transparent "plexiglass" sheet placed directly in front the animal's face. The presence of a blinking response was ascertained.

Visual Avoidance Learning. 12 trials were conducted. On the first trial the black-and-white striped board was slowly moved from a distance of about two feet towards the animal's face, finishing with a sharp tap to the animal's nose. On subsequent trials, if the subject displayed avoidance behaviors at the approach of the board in the form of flinching, grimacing, fearful vocalizations, etc., no further punishments were administered.

Depth Perception. A visual cliff (Walk & Gibson, 1961) was used to test whether the pattern-deprived animals experienced visual depth perception. The visual cliff measured 3 ft by 6 ft and was suspended 4 ft above the floor of the room which was covered with a black-and-white checkerboard pattern of 6 in-squares, identical to that directly beneath the glass of the "shallow" side.

10 trials were conducted with the "shallow" side moved alternately to the opposite side after every two trials. The

number of correct responses in which the monkey left the control board and moved to the "shallow" side were counted.

Visual Placing. Each animal was held around the midriff, suspended in the air in a prone position and slowly lowered to a flat surface. The presence or absence of appropriate placing responses was observed.

Data Analysis

The polygraphic records were scanned page-by-page and REM periods scored in accordance with the parameters typical for this phase of sleep (Meier & Berger, 1965). The onset of a REM period was defined as the point at which the EMG decreased in close association with the appearance of a relatively low voltage, fast EEG pattern together with PGO activity. Duration of REM periods were scored from their point of onset until their termination to the nearest 20 sec. Periods longer than 2 sec during which the tonic EMG level increased were not included in the REM period, nor were periods exceeding 10 sec in duration which were devoid of REMs and with EEG high voltage slow waves present.

Frequency of REMs

In the infant and juvenile monkey REM periods vary considerably from about 2 to 11 min in length (Meier & Berger, 1965). In order to make reasonable comparisons of the frequency of REMs in the same animal with increasing age and between groups, counts of REMs were made for only the first 3 min of REM periods attaining that length. Numbers of eye movements were totalled for each minute of the 3 min period.

Since small eye movements are sometimes indistinguishable from EEG activity picked up by the EOG leads, an eye movement was defined as a deflection on the horizontal EOG record which attained a height 50 μV above or below baseline. In practice eye movements were easily counted by placing a strip of transparent plastic, on which had been inscribed lines representing the baseline and 50 μV lines, over the record and aligning the ruled baseline with that of the record.

The data were subjected to analysis of variance to determine the significance of changes with age and differences between the two groups. For the purposes of age comparisons, averages of REM frequency were calculated over intervals of 6 weeks, this being the shortest interval for which samples of REM sleep were available for every animal.

Velocity of Eye Movement

The average relative velocities of eye movement during waking and REM sleep were measured from the magnetic tape recordings taken at 18 months for all monkeys including #675, and at 84 weeks of age, six weeks after the eye occluders had been removed, from monkeys #s 713 and 576.

The magnetic tape was replayed with the output of the horizontal EOG channel fed through one channel of the electroencephalograph and thence into a differentiating circuit. This circuit was constructed so that the time taken for an EOG potential to attain a set voltage of 0.3V above or below zero voltage (baseline) was proportionally represented by the voltage of a 10 msec square wave output pulse. The circuit could be

set so that it responded only to positive or negative-going deflections, representing eye movements to left or right directions. The output pulses for a given number of eye movements were averaged by summation on a Computer of Average Transients (Finemtron). Figure 1 shows the measured differences in velocity of eye movement to the left and right in control monkey #675 while it was displaying waking optokinetic responses (OKR) to a rotating striped drum. The measures obtained could only be considered as indexes of velocity of eye movement. The use of AC EOG recordings rendered it impractical to attempt to calibrate EOG reflections physically, in terms of families of curves of angular deflections at various velocities of eye movement for each subject. In addition, the slopesof the horizontal EOG deflections were dependent upon the direction of the eye movements as well as their velocity. By averaging over a considerable number of eye movements, differences in directions of eye movement among the different samples should cancel out. Therefore, the average velocities of eye movement are given in terms of the rate of voltage change (volts/sec) at the input to the differentiating circuit.

Intervals between REMs

Histograms of the intervals between successive REMs were computed from recordings taken from all subjects, including the additional control monkey #675, at 18 months of age.

This was done by replaying the magnetic tape recordings with the output of the horizontal EOG channel connected to a

single channel of the EEG machine using a time constant of 0.1 sec. The output of the EEG machine was connected to a Schmitt trigger set so that EEG deflections greater than 50 μV generated fixed amplitude square wave pulses, which were recorded on a second magnetic tape. The patterns of eye movement as represented by the pulses were then analyzed to generate first order, nonconsecutive interval histograms with bin widths of 25 and 100 msec, and ranges of 20 sec. The entire lengths of two REM periods were analyzed for each subject, except for #533 from whom only one REM period was analyzed, since its other REM periods recorded at 18 months of age contained numerous electrical artifacts.

In order to determine whether the interval histograms of the pattern-deprived and control groups differed, Chi-square contingency tables were constructed. The histograms of 25 msec bin width were divided into ten intervals. Composites of the number of occurrences in each interval for each group were compared.

To test whether the intervals between successive REMs were randomly distributed according to an exponential distribution, the g statistic was used. This statistic has previously been applied by Bartholomew (1954; 1957) to test for departures from an exponential distribution.

Results

Frequency of REMs

Although the mean rate of REM during the first three minutes of the REM period was lower for the pattern-deprived

group than for the control group at all ages (Fig. 2), this difference was not statistically significant when subjected to analysis of variance ($p>.05$, Table 1). This was due to the marked variability among individuals within the same group at every age, so that there was considerable overlap between the two groups (Fig. 2). Control monkey #605 exhibited consistently lower rates of REM than the other two members of the control group, while the pattern-deprived monkey #533 showed consistently higher rates of REM than other members of the experimental group. Both groups exhibited similar significant trends in frequency of REM with age ($p<.01$, Table 1). The rate of REM increased until 18 months of age, after which it progressively decreased until 78 weeks of age when the recordings were terminated.

In the adult monkey the rate of REM during the third minute of the REM period is usually higher than during either of the first two minutes (Berger, 1969). This was also true in the present study. It was possible that larger differences between the two groups might exist if one considered the third minute of the REM period alone. Table 2, which summarizes the analyses of variance, shows this was not the case. The differences in mean rate of REM between the two groups still failed to reach significance, although the changes with age were again significant ($p<.01$).

Velocity of Eye Movement

All of the pattern-deprived monkeys developed spontaneous horizontal nystagmoid eye movements by the time they were one

month of age (Fig. 3), which continued to be present for the duration of the study. The nystagmus was usually irregular and nonperiodic. In three of the pattern-deprived monkeys (#s 586, 539 and 698) the direction of the fast component was predominantly in one direction, not necessarily the same for each animal (Figs. 4 and 5). In the other two monkeys (#s 533 and 713) the direction of the fast component of the nystagmus would reverse from one moment to the next (Fig. 3), so that when the velocities of waking eye movement were averaged in each direction no differences occurred (Fig. 4).

The average velocities of eye movement during wakefulness and REM sleep were similar among the control monkeys (Fig. 4). But the average velocity of eye movement during REM sleep in the pattern-deprived group was considerably lower and more variable than that in the control group (Fig. 4). It is also interesting to note that the average velocity of eye movement in each direction in the pattern-deprived monkeys was similar even in those animals which showed waking nystagmus with fast component predominantly in one direction (Figs. 4 and 5). Patterns of nystagmoid eye movements were never observed during REM sleep in pattern-deprived monkeys, so that although the frequency and velocity of eye movement tended to be lower than in the control group, the overall shapes of the EOG tracings were very similar in control and pattern-deprived animals (Fig. 5).

The six weeks of visual experience following removal of the eye occluders in monkeys #576 and #713 did not produce

any change in velocity of REM in either direction (Fig. 6), however, there did appear to be individually unique changes in velocity of wakeful eye movement as a result of the visual experience. Animal #576 which had previously displayed waking nystagmus, with fast component predominantly in the left direction, after the visual experience exhibited periodic reversals of direction of the fast component, so that average velocities of eye movement in each direction were approximately equal and there also tended to be fewer slow waking eye movements (Fig. 6). Monkey #713 on the other hand, merely exhibited an overall decrease in velocity of waking eye movement in both directions, with no detectable changes in pattern of nystagmus.

Intervals between REMs

The interval histograms of REMs with bin widths of 100 msec were used in computing the χ statistic. The distribution for each REM period in every pattern-deprived and control monkey differed significantly from a random exponential distribution ($p<.05$).

The composite interval histogram of the experimental group differed significantly from that of the control group ($p<.05$; cf. Fig. 7). As might have been expected from the results of lower overall frequencies of REM in the experimental group, there was a larger frequency of very short intervals in the control group than in the experimental group (Fig. 6).

Visual behavior

The pattern-deprived monkeys were functionally blind in their gross behavior when tested at 18 months of age. They

could not walk or jump without bumping into objects, nor reach for food held a short distance away.

Following Response. The pattern-deprived group had striking deficiencies in their ability to follow moving objects with head and eyes compared to the control group. They all continued to exhibit chronic nystagmoid eye movements in the presence of the moving visual stimulus, so that no following eye movements were evident. Experimental monkeys #s 586, 598, and 576 exhibited following movements of the head to the point source of light while monkey #713 showed poor inconsistent head movements. Following head movements to the striped board and small objects were absent in all pattern-deprived monkeys. Monkey #533 did not even exhibit head movements in response to the moving light.

Blinking Response. The blinking reflex was absent in all pattern-deprived monkeys in contrast to its normal presence in all of the controls.

Visual Avoidance. Only one monkey, #576, of the pattern-deprived group exhibited visual avoidance behavior in the form of facial grimaces, screeches and turning away of the head in response to the approaching striped board. This behavior was evident on the second trial. All control animals showed consistent avoidance behaviors by the 12th trial.

Placing Response. None of the pattern-deprived monkeys showed any elements of placing responses as were appropriately displayed by the control group.

Depth Perception. All the pattern-deprived monkeys made random choices of the "shallow" or "deep" sides of the visual cliff compared with the control group, who invariably chose the "shallow" side with the exception of monkey #675, who clung to the central board and could not be forced to leave it.

Visual Behavior in Pattern-Deprived Animals following Six Weeks of Visual Experience

When the pattern-deprived monkeys #s 576 and 713 were retested, six weeks after the occluders had been removed, their visual behaviors remained the same except for some improvement in following responses in #576 and visual avoidance learning in monkey #713. Although monkey #576 still showed spontaneous nystagmoid eye movements, following movements of the head to small objects as well as to the striped board were present after six weeks of visual experience. In contrast to the total absence of visual avoidance behavior at 18 months of age, monkey #713 exhibited unquestionable visual avoidance behavior following the first trial after 6 weeks' visual experience. In spite of these improvements in visual behavior, both animals continued to show an overall picture of functional blindness by their gross behavior.

Discussion

The results of previous studies of the effects of restriction of visual input in the newborn on the development of RFFs have been somewhat conflicting. As already described, Berger, Olley, and Oswald (1962) found RFFs to be absent in

the sleep of congenitally-blind subjects, although clear EOG potentials were produced in these subjects by waking voluntary eye movements. By contrast, REMs were present in subjects with acquired blindness of 15 years or less. Offenkrantz and Wolpert (1962), also using the EOG technique to record eye movement of a congenitally-blind adult, observed REMs to be present in only a single instance during eight emergent stage 1 sleep periods recorded over two nights of sleep. Contrary results have been reported by others. Anadeo and Gomez (1966) described REMs to be present in three congenitally-blind adults and two children, from whom they also recorded the EOG. Cross, Byrne, and Fisher (1965), using strain gauges taped to the eyelids to record eye movements, also reported REMs in congenitally-blind subjects. In kittens reared in darkness until two months of age, REMs were noted to be present, but no quantitative measurements of their frequency of occurrence was made (Fishbein, Schaumburg, & Weitzman, 1966).

A decrease in frequency of REMs with age in both the pattern-deprived and control monkeys has also been observed in normal humans (I. Feinberg, personal communication). The lower frequency of REMs in the pattern-deprived monkeys compared with normal controls in this study is consistent with our earlier observations on blind humans (Berger, Oliver, & Oswald, 1962). The absence of statistically significant differences in REM frequency between the two groups was largely due to the small sample size and the considerable individual variability. Since men with acquired blindness retained REMs for up to 15 years,

it is not surprising that some REM activity might still be present in 18-month-old visually-deprived monkeys, and even less surprising in dark-reared kittens of only two months of age. However, the inconsistencies among the different studies on blind humans require explanation. The limitations of the use of strain gauges to record eye movements have already been discussed elsewhere (Berger, 1967). With this technique recorded electrical potential changes evoked by eye movement can be indistinguishable from those evoked by eyelid movement. Thus, eyelid movements in congenitally-blind subjects reported by Gross, et al. (1965), might have been mistaken for REMs, especially since eyelid movements were specifically noted to have been present by visual observation. In the study by Ampdee and Gomez (1966) it was unfortunate that examples of records showing the presence of REMs in their adult congenitally-blind subjects were not reproduced. In the two Figures which did purport to demonstrate REMs in two seven- and eight-year-old boys, the REMs were of low amplitude and in one case had a similar appearance to electrode artifacts. These could not be eliminated as a possible source of the potentials owing to the use of a central single electrode common to the horizontal EOG channels of each eye.

Our findings of similar average velocities of eye movement during wakefulness and REM sleep are somewhat misleading in light of recent measurements by Fuchs and Kow (1968), who used a considerably more accurate and reliable technique. Fuchs and Kow demonstrated that the distribution of fast and slow eye

movements in the monkey differ markedly between REM sleep and wakefulness. Furthermore, the use of an AC EOG to record eye movement in this study meant that very slow eye movements known to occur during REM sleep were not detected. However, our finding of decreased mean velocity of REMs in the pattern-deprived group compared to the control group would seem to be a reliable index of a decline in the vigor of the mechanisms underlying the generation of REMs in the pattern-deprived animals.

Our observation that interval histograms of REMs in both pattern-deprived and normal monkeys differ from a random exponential distribution confirms in the juvenile monkey similar findings in the newborn (Prechtl & Lenard, 1967) and adult human (Spreng, Johnson, & Lubin, 1968). The absence of nystagmoid REMs in monkeys displaying waking nystagmus is in accord with similar observations in adult men suffering from nystagmus of a noncentral origin (Arkin , Weitzman, & Hastey, 1966). However, recent studies of patients with waking nystagmus caused by brain lesions showed similar eye movements to be present during REM sleep (Appenzeller & Fischer, 1968).

Our observations of the behavior of visually-deprived monkeys when introduced to the visual environment are consistent with a number of earlier studies recently reviewed by Riesen (1967).

In conclusion it would seem that although REMs are intrinsically present in the newborn mammal, the maintenance of their integrity throughout later life is dependent upon patterned stimulation of the retina.

Notes

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Figure Legends

Fig. 1 Mean velocity of eye movement in left (L) and right (R) directions, and examples of horizontal EOG tracings in control monkey #675 during periods of spontaneous waking eye movement, and periods of optokinetic nystagmus responses (OKR) to the right and left.

Fig. 2 Mean rate of REM per min in pattern-deprived (open circles) and control (filled circles) groups at 6-week intervals until 78 weeks of age. Ranges are indicated by the vertical lines.

Fig. 3 EEG, EOG, and EMG recordings from pattern-deprived infant #713 at 1 week and 4 weeks of age, showing the development of waking nystagmus (R, right; L, left; F, frontal; P, parietal; O, occipital).

Fig. 4. Mean velocity of horizontal eye movement during wakefulness and REM sleep in left (L) and right (R) directions in control and experimental monkeys at 18 months of age.

Fig. 5. EEG, EOG, and EMG recordings from control monkey #641 and pattern-deprived monkey #586 during wakefulness and REM sleep. Although the pattern-deprived monkey has fewer REMs than the control monkey, note the similarities in pattern of eye movement during REM

sleep despite the sharply differing patterns of waking eye movement (R, right; L, left; P, parietal; O, occipital).

Fig. 6 Mean velocities of eye movement in left (L) and right (R) directions, and examples of horizontal EOG tracings in pattern-deprived monkeys #s 576 and 713 at 18 months of age, and 6 weeks later after their occluders had been removed. For explanation see text.

Fig. 7 Nonsequential interval histograms of experimental and control groups at 18 months of age.

Table 1

Summary Table of Analysis of Variance of Frequency of REM during the First 3 min of the REM Period

Variable	Sum of Squares	Degrees of Freedom	Mean Sum of Squares	F Ratio	Significance
Groups	3980.81	1	3980.81	2.62	n.s.
Error	9097.24	6	1516.21		
Weeks	4653.78	12	387.82	4.44	<.01
Groups x Weeks	1381.11	12	115.09	1.32	n.s.
Error	6286.88	72	87.32		

Table 2

Summary Table of Analysis of Variance of Frequency of REM during the 3rd minute of the REM Period

Variable	Sum of Squares	Degrees of Freedom	Mean Sum of Squares	F Ratio	Significance
Groups	5083.60	1	5083.60	3.46	n.s.
Error	8812.45	6	1468.74		
Weeks	6300.95	12	525.08	4.95	<.01
Groups x Weeks	1495.31	12	124.61	1.17	n.s.
Error	7638.56	72	106.09		